A REEXAMINATION OF THE SIMILARITIES BETWEEN THE FRESHWATER FISHES OF AFRICA AND SOUTH AMERICA

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The similarities between the freshwater fishes of South America and Africa have long attracted attention. Ichthyologists have frequently been blunt about implications. Eigenmann in 1910 (1910b, p. 1) wrote, in part : " ... the fauna of tropical South America has had a common origin with that of Africa ". Regan in 1922 (p. 206) was somewhat more specific : " It seems reasonable to believe that in early Cretaceous times, South America and Africa formed one continent... '. What Regan considered " reasonable " in 1922 seemed quite unreasonable to a large number of people in the ensuing 40 years, and in the controversy that developed, the underlying and unsolved problems of fish distribution in Africa and South America were lost from sight. Though these problems will not be solved here, they will at least be brought to light and examined, and some evidence bearing on them will be provided. (Only the tropical fishes will be considered ; the very small temperate-zone freshwater fish faunas of South America and Africa present different zoogeographic problems.)

The basic distributional data for the freshwater fishes of Africa and South America are readily available, e.g., in Darlington (1957). The only catalogue covering all South American freshwater fishes remains that of Eigenmann (1910a). Poll (1957) provided an account of the African freshwater genera, which supersedes Boulenger's (1909-1916) " Freshwater Fishes of Africa ".

The three large tropical freshwater fish faunas of the world today are those of South America, Africa and Southeast Asia, and it is with the interchanges among these three that the present paper will be concerned. Certain freshwater groups occur today in all three major areas, but Africa has some major groups in common *only* with Southeast Asia and another *only* with South America. Finally, both South America and Africa have endemic groups. The problem is to provide a coherent causal explanation for these various distributional patterns.

In dealing with the zoogeography of freshwater fishes, the first question that arises is that of barriers to dispersal. Where the fish faunas of two or more separate continents are dealt with, a major barrier is the sea. However, with adjacent continents, it becomes advisable to examine the possibility of other types of barriers as well. Intercontinental land connections do not necessarily mean that freshwater fishes have been able to cross them. For example, freshwater fishes have been very slow to move along narrow, high intercontinental connections with few longitudinal watersheds, such as that between North and South America (Miller 1966, Myers 1966). Again, the land connection between Africa and Southeast Asia now forms an almost impassable barrier between the fish faunas of these two regions. This appears to be primarily because of the aridity of much of the Middle East today, and such fishes as now occur there (see, for example, Berg, 1949, Kosswig 1952, Pellegrin 1928, Steinitz 1954) seem to be chiefly Palearctic forms, probably left behind from wetter Pleistocene periods. One factor of possible but unknown zoogeographic significance is that fishes with the greatest ability

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to cross montane or climatic barriers may be of a quite different sort from those best able to surmount marine barriers to freshwater fish dispersal.

As to marine barriers, much has been written on the subject (cf. Myers 1949), which is considerably more complex than a casual reading of the literature might suggest. In the first place, the physical environment, in at least certain areas, complicates matters by blurring the distinction between fresh waters and the sea. For example, surface lenses of fresh water may be carried well offshore from the mouths of such rivers as the Amazon. Again, where the scacoast is bordered by marshes, the possibility that at least certain freshwater fishes can work along the inner borders of the marsh areas from one river mouth to the next is greatly enhanced.

As for the fishes themselves, there appear to be few, if any, freshwater groups that cannot tolerate brackish or salt water. A rather brief search of the literature provides brackish-water or marine records for representatives of all but two of the larger groups of African and South American freshwater fishes. (The two exceptions are the mormyrids and gymnotids, but Mr. Cichocki tells me that he has taken *Gymnotus* in brackish water). The literature records are as follows :

— Osteoglossiformes. The fossil *Brychaetus*, if it is really an osteoglossiform fish (see Patterson's paper in this volume) was marine.

— Cypriniformes (= Ostariophysi of older authors). A Japanese cyprinid, *Tribolodon taczanowskii*, appears to have a sea-going anadromous form (Okada 1960). Miller (1965) has taken the American characin, *Astyanax*, from a mangrove area in Mexico, and Chardon (1967) lists brackish-water records for two African characins. Chardon also provides marine or brackish-water records for four families of catfishes, and Lowe (1962, p. 687) adds the Pimelodidae.

— Cyprinodontiformes. Marine records are too numerous to cite.

— Perciformes. Among the nandids, *Nandus marmoratus* inhabits " fresh and brackish water of India and Burma " (Day 1889, p. 82). Among cichlids, at least one species of *Tilapia* is able not only to live, but breed successfully in sea water.

— Synbranchiformes. *Synbranchus*, at least in the Indo-Australian region, inhabits " fresh and brackish water " (Weber & de Beaufort 1916, p. 416).

That salinity alone is no lethal barrier to freshwater fish groups is sufficiently shows by the preceding records. Nevertheless it would be strange if the marine environment, which differs from fresh water not only in salinity, but also in the nature of its food supplies, predators, and cover, did not form at least a partial barrier to the dispersal of freshwater fishes. Asa working hypothesis it might be suggested that because the sea differs more in the totality of environmental factors from hill streams than it does from large rivers and swamps, the sea would provide a greater barrier for hill-stream fishes than for forms normally living in large rivers and swamps. That such is the case at least within the catfish family Aspredinidae is borne out hy Myer's (1961) paper.

In the final analysis, the best measure of the extent to which the sea has formed a barrier to freshwater fish dispersal is the distribution of the fishes. For exemple, the presence of native cyprinodonts and a synbranchid on West Indian islands (Myers 1938) and of cichlids in the West Indies and Madagascar suggests that a marine environment does not present a very severe barrier to the dispersal of these fishes. For the other South American and African freshwater fish groups, it would seem best to hold open the possihility of at least a limited coastwise dispersal for some members.

From this point on, the discussion will be centered on a single order, the Cypriniformes (Ostariophysi). There are several reasons for this procedure. The Cypriniformes is the largest order of freshwater fishes, with approximatively 6,200 species (Cohen 1970), and its members dominate the tropical, and for that matter temperate, waters of all continents except Australia. The other tropical fishes and their distribution are thus to a greater or lesser extent peripheral ot the cypriniform fishes and hence to the subject at hand. Finally, cypriniform classification and zoogoegraphy (Regan 1922, Rossi 1951, Chardin 1967) have already received considerable attention. The basic information regarding the Cypriniformes will be summarized briefly. (This does not seem the proper place to review in detail the large amount of recent systematic work on cypriniform fishes. Suffice it only to say that working out phylogenetic lineages in a group with as much adaptive radiation as has occurred in the Cypriniforms is a difficult process, and that much remains to be done).

That the cypriniform fishes are monophyletic is strongly indicated by the presence of a complicated and unique set of Weberian ossicles in all individuals, and by other less trenchant and less constant features. The cypriniform fishes are divided into two morphologically well-separated groups : the siluroids (catfishes) and the cyprinoids (characins, gymnotids or " electric eels " and the cerps and their allels). Both of these suhorders are abundantly represented throughout the tropical end temperate freshwaters of the continents other than Australia. Despite the marine records (see above) and the two marine catfish families, there seems every reason to believe that the origin and diversification of the cypriniform fishes took place in fresh water (for a different hypothesis, see Patterson's paper in this volume).

The catfishes seem to represent a tremendous adeptive radiation around one main theme. The most primitive living catfish is *Diplomystes* of the Andean foothills of Chile and Argentina, where it is presumably relict. Aside from *Diplomystes*, the hesic catfish stock today is represented by a group of closely related families — Ictaluridae, Pimelodidae and Bagridee — with the ictalurids restricted to North America, the pimelodids to South America, and the bagrids to Africa and Southeast Asia. Most of the other catfishes including the marine forms, are thought to be derived from one of these three families. The only non-marine catfish families of North and South America ere restricted to the single continent in which they occur, but the non-merine catfish families of Africa are partly endemic and partly shared with Southeast Asia. In the latter area there are three other families that are either endemic or extend into the Palearctic.

The cypronoids have a very different set of groupings from the catfishes, both taxonomically and zoogeographically. The suhorder is represented by three distinct clusters of families. The smallest of these, the gymnotids, is restricted to South and southern Central America. The characins occur in Central and South America and Africa, hut are more diversely represented in South America. The cyprinids (carps, etc.) and their allies are found in Southeast Asia, the northern continents, and Africa. They show maximum diversification in Southeast Asia.

The hasic zoogeographical problems presented hy the Cypriniformes are, I think, two. First, if the more generalized catfish types occur all over the world, why are the cheracins (with the exception of a few recently arrived Middle American forms) restricted to South Americe and Africa ? Second, if the characins occur in South America and Africa, then why are gymnotids restricted to South America ? The rest of this paper will deal with these questions.

The varying distrihution patterns of the four main cypriniform groups — catfishes, characins, gymnotids and cyprinids — might be explained hy differences in dispersal ability, hy differences in age, or hy a combination of both factors. At the ono axtreme, it might he hypothesized that all four groups evolved at ahout the same time from a single widespread ancestor, but that the catfishes have had better dispersal ahilities than the cyprinids and characins, which in turn wero hetter able to spread then the gymnotids.

There is at least some circumstantial evidence hearing on on this hypothesis. The catfishes are the only one of the four main cypriniform groups with marina families, and one of these, the Ariidae, now occurs along tropical shores from the west coast of the Americans to Ms dagascar, Australia and the Philippines. Despite the fact that the Ariidae is the oldest recorded catfish family (see helow), it does not seems morphologically possible to derive the other catfishes from it. Also the fact that the Ariidae and the marine Plotosidae ere the only cypriniform families present in Madagascar and Australia suggests that other catfishes have been more, if not entirely, restricted in their dispersal by marine harriers. In short the evidence of the msrine catfish families at hest weakly supports the hypothesis that catfishes were better ahla to cross marine harriers than other cypriniform groups. Furthermore, the non-marine catfishes do not seem to extend farther out into peripheral (as contrasted with isolated) island groups such as Japan and the Philippines than the cyprinids do.

In any event, a oypriniform group that does not agree well with the thesis of differential dispersal ability is the gymnotids. It is difficult to comprehend why, if the characins and gymnotids are about equally old, the characins aro now in Africa and the gymnotids are restricted to South America.

At tha other axtreme of the spectrum of possible dispersal-historical hypotheses is the postulate that all four mein cypriniform groups had ahout equel dispersal abilities hut that the catfishes evolved

first and hence were able to make use of land connections unavailable to the other, later cypriniform groups; that the characins and cyprinids evolved somewhat later, and that the gymnotids were the last of the main cypriniform groups to appear. This thesis too, raises some difficult questions. In the first place, there is the matter of cypriniform phylogeny.

If it is hypothesized that the catfishes were the first cypriniform group to evolve, then there is the implication that the other cypriniform groups arose from the catfishes. But the modern catfishes that are spread all over the world today are clearly a specialized group that has given rise to nothing except other catfishes, certainly not to the characins, gymnotids and cyprinids. But if a common ancestor for the groups is assumed, and the further assumption is made that the catfishes are the earliest specialization from this ancestor, then the question arises of what was prototype of the characin-gymnotid-cypriniid group doing while the catfishes were spreading around the world?

In the absence of any satisfactory explanation for the present distributions of the four main cypriniform groups, a preliminary working hypothesis will be suggested here that combines historical and ecological factors. It seems best to start with the results of my own attempts to determine the phylogenetic sequence of events in the cypriniform fishes from the morphology of modern forms. (The morphological bases for these results will be published elsewhere).

That the catfishes, gymnotids and cyprinids have all become specialized in different ways has long been clear. Because the Characins do not show as many obvious and drastic specializations as the other three groups, it is assumed, tacitly or explicitly, that the characins show the greatest similarity to the ancestral cypriniform stock of any of the four groups. My own work does not indicate a different conclusion, but it strongly suggests that the forms usually considered to be the most generalized of the living characins — *Brycon* (Weitzman 1962, Alexander 1965) and *Hepsetus* (Roberts 1969) — are highly specialized, at least with regard to structures associated with feeding, and that the ancestral characin was a small-mouthed form with small, undifferentiated teeth (Gosline 1973). It may well have been a small-sized, small-stream, bottom-feeding fish. Possibly the South American hill-stream characin genus *Characidium* approximates such an ancestral characin, though *Characidium* has probably become secondarily specialized for a hill-stream environment. (Unfortunately, the anatomy of the genus is not well known).

So much for the ancestral characin. Beyond lies the question of whether such a fish could have served as an ancestor for the other cypriniform groups as well. There is no serious morphological reason why the other cypriniform groups could not have evolved from such a form. However, it is highly possible that the ancestor of all four groups of Cypriniforms had one or more of the characteristics of the catfishes and/or cyprinids that are not found in modern characins, e.g., 6 or 7 branchiostegal rays, a maxillary barbel, no cranian fontanel, no adipose fin. This ancestral cypriniform morphological type could, provided it occured in both South America and Asia, have given rise to each of the other cypriniform groups. (The preceding sentence deals only with morphological potentiality; it is not a statement, or even an implication, of what actually occured).

The subordinal division of the Cypriniformes between the catfishes in one suborder and all of the other members of the order in a second is based on degree of morphological differentiation, and it is generally assumed that the tremendous morphological distance between the catfishes and the other cypriniform fishes developed very early. However, Alexander (1965) has shown, to my mind quite convincingly, that the many catfish peculiarities are mostly adaptive traits associated with a few basic changes in mode of life. That such changes may take place rapidly is well known. The question is when did the catfish specializations develop relative to the differentiation of other cypriniform groups? There is no decisive evidence on this point, though catfish branchostegal structure and a few other minor features suggest that the catfishes diverged from the main cypriniform stock before the other three groups became separate from one another.

Let us assume, with the majority of authors, that the catfishes split off before the other cypriniform groups differentiated. Then, as already noted, one might attribute the wide distribution of the basic catfish stock to the availability of land connections which were no longer present when the characins, cyprinids and gymnotids became differentiated. But this brings us back to the question of what the ancestors of the characins, cyprinids and gymnotids were doing while catfishes were dispersing?

A theoretical ecological hypothesis might explain the difficulty and also mitigate to some extent the stigma of postulating special land bridges for catfishes. Assume, on the basis of at least some fossil evidence, e.g., in the Green River Eocene (Lundberg and Case 1970), a dominance of predaceous osteoglossiform fishes preceding the present cypriniform radiation. Assume a small-mouthed, perhaps hill-stream cypriniform ancestor. Now as contrasted with characins, gymnotids and cyprinids, the catfishes developed, apparently at an early date (Lundberg and Case 1970, Peyer 1928), highly specialized defensive spines (Alexander 1965). The hypothesis offered here is that these fin spines may represent an effective defense against large predators that may have permitted the catfishes to develop a big-river habitus earlier than the characins, gymnotids and cyprinids. Certainly, the world-wide ictalurid-pimelodid-bagrid group is made up of primarily riverine fishes today, and one with not infrequent marine and semi-marine records. If the assumptions made here are correct, it seems possible that the catfishes, ecologically as well as historically, may have been able to take advantage of lowland dispersal routes earlier and more effectively (Rossi 1951) than the ancestral characins, gymnotids and cyprinids. In short, the catfishes might have been able to disperse along lowland and perhaps coastal routes while the ancestor of the characin-gymnotid-cyprinid lineage was still restricted to the smaller streams.

As to the characins, gymnotids and cyprinids, the present distributions of these three groups, as previously noted, are very different. The characins provide the best fish evidence for formerly adjacent South American and African continents. If this evidence is valid, and there is little reason to think that it is not, South America and Africa cannot have separated until after the characins evolved. Though there are today characins with small mouths and simple teeth, as postulated for the ancestral type, the great majority of modern characins, both in Africa and South America, have a strong and complex shearing or biting dentition and relatively large, powerful jaws. Indeed, in Africa today, the cyprinids seem to provide the bottom-feeding counterparts of the characins with that mode of life in South America (Roberts 1972).

The gymnotids are restricted to South America. They form a highly peculiar, though rather abundant and diverse group of fishes whose specializations seem to be mostly associated with electric-field production and reception (Roberts 1972). In this, the gymnotids appear to represent the ecological counterparts of the African mormyrids, though the phylogenetic relations of the two groups are very different. Because of the separate development of these two groups in the two continents, it is assumed that, despite their high degree of specialization, they have evolved since Africa and South America became separated. The assumption will be accepted here, but with misgivings.

The history of the cyprinids and their allies is more complex. The greatest diversity of modern forms is found in the fresh waters of Southeast Asia, and there is nothing to indicate that this area was not also their center of origin. From this center, the cyprinids and their allies appear to have spread into the north temperate regions and they now occur throughout such regions of the Palearctic and Nearctic. The more tropical elements reached Africa and now occur throughout Africa. Presumably, the arrival of the cyprinids in Africa occured after the separation of Africa and South America, for there are no cyprinids in South America. Today, the interchange of tropical cyprinids, and indeed of most other tropical freshwater fish groups, between Africa and Southeast Asia has again been eliminated, as previously noted.

It seems advisable at this point to comment on non-cypriniform fishes. Aside from forms like the cichlids which can and have crossed marine barriers, the South-American African non-cypriniform fishes may be divided into three main components for purposes of zoogeographic analysis. First there are the two groups, presumably older than the cypriniform fishes, represented in Australia as well as in Africa and South America today : the lungfishes and osteoglossids. Second, there are a number of African groups endemic to that continent today. Among these, such groups as the polypterids may well be relicts of a once wider distribution, but this explanation will not serve for the mormyrids, which must, perforce, be considered as young (see above). Third, there is a fairly large group of higher teleosts that have apparently entered Africa from a South-east Asian center of development, some or all of which may have entered Africa at the same time as the cyprinids : Nandidae, Anabantidae, Channidae, Mastacembelidae and Synbranchidae. Two of these — the Nandidae and Synbranchidae — are also in South America today. *Synbranchus* is, however, represented in the

West Indies, and should probably be excluded from consideration here. It is mentioned because, aside from the insular records, it shows much the same general distribution pattern as the Nandidae.

Based primarily on the distribution of modern cypriniform fishes the following sequence of events in terms of fish dispersal may be postulated :

I. — The loss of a connection between Australia and other continental landmasses. (That such connection once existed is strongly suggested by the representation in Australia today of two freshwater fish groups : lungfishes and osteoglossids).

II. — The loss of an accessible interconnection, so far as tropical freshwater fishes are concerned, between Southeast Asia and the South American-African area. (Such a separation is postulated to permit the development of the cyprinids and their allies in Southeast Asia and the characins in the African-South American area).

III. — The separation of Africa and South America, followed by :
   a. The evolution of the gymnotids in South America.
   b. The evolution of the mormyrids in Africa.
   c. The development of an interchange of fishes between Southeast Asia and Africa. (This interchange seems to have consisted mostly, perhaps entirely, of the entry of Southeast Asian fishes into Africa, with little, if any, movement of African fishes into Southeast Asia).

IV. — The loss of a possibility of interchange between the tropical freshwater fishes of Southeast Asia and Africa.

Consideration of the cypriniform fossil record has been deferred until this point because the fossil record, at least up to now, is chiefly of value in placing time limits before which certain aspects of cypriniform distribution must have occured. Regan (1922, p. 206) wrote : " The palaeontological evidence as to the past history of Ostariophysi is very imperfect, but several important facts emerge. These are that none of the families is known to have had in former times a more extended range than at present, that some highly specialized families were in existence in the Eocene, that the characteristic Nearctic families, Catostomidae and Amiuridae, were already established in North America in Eocene times, and finally that nearly all the fossils are generically identical with living species and that the few extinct genera are not very clearly distinguished from modern ones ".

Most of the fossil records since 1922 merely bear out Regan's statements. Thus, White has described (1934) Eocene bagrid catfishes from Nigeria and (1931) a fossil cyprinid belonging to the modern genus *Blicca* from the Lower Eocene of the London Clay. There are, however, two Eocene records that lie outside the present ranges of the groups involved. One is that of Lundberg and Case (1970) for an ictalurid catfish from the Green River beds of the western United States ; catfishes, aside from introductions, are absent from the western slope of North America today. The other is the record of characin teeth from France provided by Cappetta, Russell and Braillon in the present volume.

Aside from a possibly siluroid otolith (Frizzell 1965), there are still no Mesozoic records of the Cypriniformes. Indeed, a catfish attributed to the marine Ariidae (Casier 1960), is still apparently the only Palaeocene record. Yet, it is obvious, as Regan indicated, that the principal evolution and dispersal of the main cypriniform groups (except the gymnotids, for which there is no fossil record) had already taken place in the Lower Eocene. That the marine Ariidae were already widely dispersed by Eocene time is indicated by records attributed to them from the Wyoming Green River (Lundberg and Case 1970), the London Clay (Regan 1922), the Fayum of Egypt (Peyer 1928), and the Congo (Casier 1960).

Two points regarding the zoogeographic implications of the characin teeth described elsewhere in the present volume seem relevant here. In the first place, if the thesis regarding characin phylogeny advanced in the preceding pages is correct, any teeth that could be recognized as characin teeth would be from a characiu of an advanced type. Second, there has always been the puzzling question of why, if cyprinids came into Africa from Southeast Asia, the characins did not leave Africa by the same route. In southern North America, it is the characins that are invading area occupied by cyprinids and not vice versa (except for human introductions). That cyprinids and characins can and do live in the same waters is indicated by Africa, though there the two groups do tend to separate

ecologically (Roberts 1972). So the basic question of why the characins never got out of Africa is merely changed by the French records to a question of why the dispersal from Africa eventually failed.

What the fossil records show with relation to the sequence of events outlined above, is that cyprinids and their derivatives had already arrived in England and America in Eocene times. Though the fossil record does not bear evidence on the matter, it seems probable that the cyprinids would also have arrived in Africa by then, too. But cyprinids are not in South America. The fishes, therefore, like so many animals and plants, suggest a pre-Eocene separation for South America and Africa. Even this much of a conclusion is based on fossil evidence, and only further fossil evidence can provide a more precise timing, at least, so far as fishes are concerned.

As to the early barrier to the interchange of fishes between the tropical freshwater fishes of Southeast Asia and Africa while Africa and South America were adjacent, there seems no way to postulate the nature of this barrier. Perhaps it was a marine barrier or perhaps it was of a climatic or physiographic nature. Possibly a close analysis of the fishes of the Indian Subcontinent would provide some clue to the matter, but this lies outside the scope of the present paper.

With regard to the somewhat later interchange between the tropical fishes of Southeast Asia and Africa, one curious point deserves mention. The largely one-way migration of Southeast Asian fishes into Africa in presumably pre-Eocene or early Eocene times has already be mentioned. There is, however, one American-African group, the Cichlidae, that seems to have moved east to Madagascar and southern India but not beyond. The cichlids appear to be a relatively advanced group of higher teleosts and they do cross marine barriers. Despite this, it is perhaps significant that the later eastward route of the cichlids to India is apparently quite different from the earlier westward route of the cyprinids from Southeast Asia to Africa.

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DISCUSSION

après la communication du Prof. W. Gosline

Intervention du Professeur M. Chardon.

1re Question : Pensez-vous que les Gymnotoidei soient plus ou moins anciens que les Characins connus aujourd'hui ? Un travail en cours (entrepris avec M. de la Hoz) montre que les Gymnotoidei présentent un appareil de Weber au moins aussi primitif que celui des Characoidei. Nous avons aussi remarqué chez les Gymnotes l'absence des fosses postérieures du crâne des Characins.

Réponse : In many respects the gymnotoids are highly specialized fishes. Partly because the few gymnotoid characters I have examined could have been derived from the characin condition and partly because the gymnotoids are restricted to South and Middle America today, I had assumed they were characin derivatives. Admittedly, my bases for this assumption are weak.

2e Question : Ne pensez-vous pas que les Ostariophysi sont plus anciens que le début du Tertiaire ? Il est à noter que les premiers restes de Silures, qui datent du Paléocène, appartiennent à des Ariidae qui, anatomiquement, sont certainement spécialisés et doivent être rattachés aux Bagridae.

Réponse : I wholly agree with Professor Chardon on this matter.

Intervention du Professeur Kosswig.

Question :

Si l'hypothèse d'un ancêtre commun de tous les Osteriophysi est bien fondée et l'ichthyofaune de l'Amérique du Sud et de l'Afrique est en bon accord avec celle-ci, il faudrait supposer que les Cyprinides, comme représentants orientaux des Characides, se sont formés aux Indes (péninsule indienne). Deux faits ne sont pas en accord avec cela : 1) l'existence de genres modernes de Cyprinides dans l'Eocène de l'Europe; 2) Le centre de diversité et d'une radiation adaptive des Cyprinides se trouvent dans le SE de l'Asie, ancienne part de Laurasie. Un fait peut diminuer ces divergences : il y a plusieurs genres de Cyprinides, qui passent au moins une partie de leur vie en eau saumâtre : p.e. dans la mer Noire, dans la Baltique et la mer chinoise. Pour prendre usage de ce fait il faudra attendre des résultats des recherches des géophysiciens concernant l'interprétation des relations entre la péninsule indienne et le SE de l'Asie pendant le Crétacé.

Réponse :

So far as I know, the problem of the origin and dispersal of cyprinids is badly in need of careful examination. The geographic and paleogeographic factors that Professor Kosswig mentions are one aspect of the problem. More discouraging to me is the fact that we still do not know the various lines of phylogenetic development within the family Cyprinidae.

Intervention du Professeur P. Vandewalle

Question :

Suite à l'intervention du Professeur Monod, je pose la question suivante : la présence de Cichlidae en eau salée le long de la côte africaine et les possibilités de vie en eau de mer d'un *Tilapia* introduit en Asie, sont-elles suffisantes pour expliquer un passage entre l'Afrique et l'Amérique du Sud ?

Réponse :

The distribution of cichlids is of great zoogeographic interest, but I have left it out of consideration here because of the possibility Professor Vandewalle mentions that the cichlids somehow managed to cross the Atlantic.